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corresponding parts of the other twin. It is evident from the experimental data, notably that of Muller,<sup>4</sup> that new connections are not formed with any torn fragment of chromosome which happens to come into the proper position, but that connections are always formed at exactly corresponding points with homologous systems of genes.<sup>5</sup> It is like the replacement of one chemical radicle with another within a complex organic molecule and it seems highly probable that such is its real nature.

¹ The distances shown in Morgan's chromosome map in excess of 50 (admittedly not obtained experimentally but only by summation) are therefore too large. Accordingly, if one clings to the assumption that the arrangement of the genes is linear, it must be, not that the longer distances are too short, as Morgan has assumed, but that the short distances are too long. Therefore, any hypotheses framed to account for an apparent shortening of the long distances are superfluous. The long distances given by direct experiment are long enough; they approach the limit of the possible, viz., 50%. Thus in table 65 of Morgan and Bridges, we find the following high cross-over percentages given by direct experiment:—yellow-bar, 47.9; white forked, 45.7; and white-lethal sc, 46.0. What is needed therefore, if the linear arrangement hypothesis is retained, is a secondary hypothesis to explain why the short distances given by experiment are too long.

But if we abandon the hypothesis of linear arrangement, all secondary hypotheses are unnecessary. The experimentally obtained cross-over percentages may be accepted at their face value, which in every case fall within the limits of the possible, 0 and 50.

- <sup>2</sup> Morgan, T. H., and Bridges, C. B., Sex-linked inheritance in Drosophila. *Carnegie Inst. Washington, Publ.*, No. 237, 1916, (88 pp., 2 pl.).
  - <sup>3</sup> Weinstein, A., Genetics, 3, 1918, (135-172).
  - <sup>4</sup> Muller, H. J., Amer. Nat., Lancaster, Pa., 50, 1916.
- <sup>6</sup> The case of 'deficiency' studied by Bridges (*Genetics*, 2, pp. 445-460, Sept. 1917) forms an apparent exception to the rule. Here a certain segment of the linkage system was as regularly wanting as it is commonly present. The regularity of the process, however, shows that the principle of union at particular points still holds. In the deficiency race, a new and simplified linkage system had been established and this persisted.

## THE LINKAGE SYSTEM OF EIGHT SEX-LINKED CHARACTERS OF DROSOPHILA VIRILIS (DATA OF METZ¹)

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In an earlier paper it has been shown that the arrangement of the genes in the sex-chromosome of *Drosophila ampelophila* is probably not linear, and a method has been developed for constructing a model of the experimentally determined linkage relationships. From such a model one may by direct measurement ascertain what other undetermined linkage values are likely to be. In order to test the utility of this method, it is desirable that it be tried out as widely as possible and the results for different cases compared with each other. For such use, suitable material is found in a paper by Metz<sup>1</sup> dealing

with the linkage relations of eight sex-linked characters in *Drosophila virilis*, a species distinct from *D. ampelophila*, which has been so exhaustively studied by Morgan and his pupils. Of the eight characters studied by Metz, two agree morphologically and in their linkage relations with each other, with similar characters of *D. ampelophila*. The six others have no exact counterpart among the known mutations of *D. ampelophila*. The two characters in question are yellow body and forked bristles. Yellow body, in both species, lies at the extreme, 'zero' end of the linkage system. Forked, in both species lies at a distance of 40 or over from yellow. In *D. virilis* the distance is exactly 40, according to the observations of Metz; but in *D. ampelophila*, according to Morgan and Bridges, the distance is about 6 or 7 units greater. But inspection of figure 1 (p. 29) shows that this estimate is probably too

TABLE 1

GENES	TOTALS	CROSS-OVERS	PERCENTAGE CROSS-OVERS
Yellow-frayed	308	4	1.3
Yellow-vesiculated	3,548	621	17.4
Yellow-magenta	3,049	1,157	38.0
Yellow-hairy	162	65	40.1
Yellow-forked	3,781	1,510	40.0
Yellow-glazed	1,328	591	44.5
Yellow-rugose	1,060	502	47.3
Frayed-vesiculated	296	55	18.6
Vesiculated-magenta	2,799	944	33.7
Vesiculated-forked	3,761	1,395	37.1
Vesiculated-glazed	877	359	42.1
Vesiculated-rugose	1,696	729	42.9
Magenta-forked	2,529	95	3.7
Magenta-rugose	824	197	23.9
Hairy-forked	162	5	3.1
Forked-glazed	749	4193	25.7
Forked-rugose	1,158	321	27.7

high, since the wire joining white (W) with forked (F) in the model is too long to harmonize fully with other linkage-values given by Morgan and Bridges, the wire being curved. The distance yellow-forked is not given by Morgan and Bridges but it evidently should be about one unit greater than the distance, white-forked, which is given as 45.7. If this estimate of the distance is too high, as figure 1 indicates, then the distance yellow-forked is probably not very different in the two species of Drosophila and will be found to be not far from 40 in both.

The linkage values found by Metz for the eight sex-linked genes of *D. virilis* have been gathered from his several tables, averaged and brought together in table 1 herewith. They form the basis of the reconstruction shown in figures 3 and 4.

Metz, adopting Morgan's system of linear grouping, shows the eight genes in a linear chain more than 80 units long, although the greatest distance experimentally found between any two genes is 47.3 (yellow-rugose). This discrepancy, like the similar ones observed in *D. ampelophila*, shows the inadequacy of the hypothesis of linear arrangement. For the maximum possible

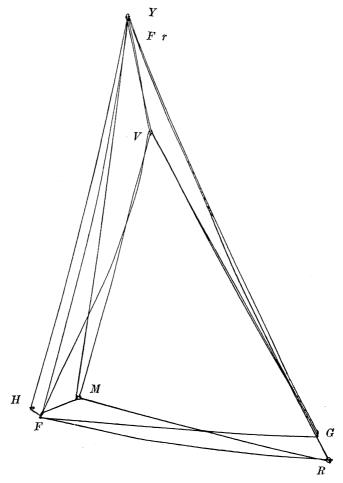


FIG. 3. MODEL SHOWING RELATIVE POSITIONS OF GENES OF 8 SEX-LINKED CHARACTERS OF DROSOPHILA VIRILIS

cross-over percentage is 50 and this is in no case exceeded by data given by direct experiment.

Reconstruction in three dimensions (figs. 3 and 4) shows even more clearly in this case than in that of D. ampelophila, that a linear arrangement is out of the question. The reconstructed figure is roughly in the form of a tetrahedron. Figures 3 and 4 are views taken at right angles to each other corre-

sponding with the two views given for *D. ampelophila* in figures 1 and 2. The eight genes lie in four groups at the four apices of the figure, in groups of 2, 3, 2, and 1 respectively. The figure has a very definite and rigid form, for geometrical reasons. Three additional linkage relations should be known to determine fully the position of certain of the genes within their respective

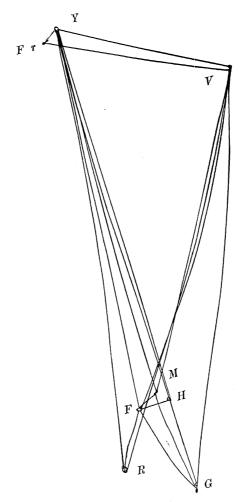


FIG. 4. MODEL SEEN AT RIGHT ANGLES TO FIGURE 3

groups. These are magenta-hairy, glazed-rugose, and frayed-forked (or frayed-glazed), where the figures show connecting wires to be wanting.<sup>2</sup> Given these missing connections, the form of the model would be very fully determined in every detail. Any newly discovered sex-linked gene of *D. vivilis* having been located with reference to three of these eight genes, its rela-

tions to all the others could be predicted by direct measurement from the model.

- <sup>1</sup> Metz, C. W., Genetics, 3, 1918, (107-134).
- <sup>2</sup> From measurement of the model, it may be predicted that the cross-over percentage between magenta and hairy will be about 4 or 5, and the glazed-rugose percentage about the same, probably a little greater. The position of frayed in the system is not fully determined, as only two linkage relations of frayed are known. But it may be predicted, from measurement, that the frayed-forked cross-over percentage will lie between 39 and 41, and that frayed-glazed will lie between 43 and 46, provided of course that the relations given in table 1 have been determined with sufficient accuracy.

## THE CAUSE OF PROLIFERATION IN BEGONIA PHYLLOMANIACA

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The cause of the excessive production of adventive shoots on the leaves and internodes of this plant (a very strange phenomenon) is attributed to excessive loss of water, due to woundings or other causes. Usually in regeneration the response is not far from the place of injury, here it may be at a long distance from the wounded part, e.g., roots wounded and response in the top of the plant, although a direct response from the injured part can also be obtained. The paper will be published in full in *The Journal of Agricultural Research*. The following is a synopsis:

- 1. Ordinary begonia leaves when detached from the plant and pegged down on moist sand develop roots and shoots from cut places and this method is used by gardeners for the propagation of begonias. Many other plants are propagated in this way, e.g., the hyacinth from bulb scales.
- 2. But the leaves and shoots of this begonia proliferate while still attached to the plant.
- 3. They will proliferate on the plant very freely when wounded, making small forests of shoots on the thickened red lips of the wound if the wounds are made in quite young tissues, but not otherwise (young leaf blades were used).
- 4. They will frequently proliferate in the top parts of cuttings (on leaves and internodes) especially if the cuttings are dried for a day or two before planting.
- 5. They will proliferate most astonishingly at the top of the plant (both from leaves and internodes) if the roots are wounded, but here again only quited young tissues can be shocked into the production of such shoots. This is the most striking fact I have discovered, viz., that the prolification may occur at a long distance from the place of wounding and must be from young